

4. On the Fossil Teleostean Genus *Rhacolepis*, Agass. By A. SMITH WOODWARD, F.Z.S., F.G.S., of the British Museum (Natural History).

[Received June 7, 1887.]

(Plates XLVI. & XLVII.)

Among the numerous fossil fishes named and briefly noticed by Agassiz during the preparation of his great work 'Recherches sur les Poissons Fossiles,' but reserved for adequate description in the contemplated supplements which unfortunately never appeared, are some interesting specimens from the north of Brazil, displaying the characters of an extinct generic type, mentioned under the name of *Rhacolepis*. Of these the British Museum now contains an extensive series, enriched especially by the recent acquisition of the Egerton and Enniskillen collections; and as materials are thus provided for a tolerably complete elucidation of the ancient fish they represent, the present seems a favourable opportunity for completing the original diagnoses. The majority of the fossils were actually examined by Agassiz himself, and several bear his MS. labels, so that it is possible to recognize the various species he intended to establish. And a careful study of the whole series has lately revealed some novel facts in regard to the affinities of the genus, which appear to have hitherto escaped observation, and render it of considerable interest to the zoologist.

The fossil fishes in question, together with four or five other genera, are discovered in calcareous nodules, of concretionary origin, scattered upon the hill-sides in the neighbourhood of Barra do Jardim, Serra de Araripe, North Brazil, and the first published allusion to them appears to occur in the record of Spix and Martius's travels at the beginning of the present century¹. About 1840 many specimens were collected by Mr. George Gardner, of Glasgow, who submitted them to Agassiz, and briefly described the circumstances under which they were met with²; and these, probably, form the greater part of the Museum collection at the present time. Still others were brought under Agassiz's notice by MM. F. Chabrilac and Elie de Beaumont, and formed the subject of a lengthy report published in the 'Comptes Rendus' for 1844³. Nearly thirty years later, Professor C. F. Hartt added further remarks upon the geological evidence as to the age of the nodules themselves⁴; and

¹ J. B. von Spix and C. F. von Martius, 'Reise in Brasilien,' 1823-31, Atlas, pl. 22. fig. 5.

² G. Gardner, "Geological Notes made during a Journey from the Coast into the Interior of the Province of Cearà in the North of Brazil," Edimb. New Phil. Journ. vol. xxx. 1841, pp. 75-82.—L. Agassiz, "On the Fossil Fishes found by Mr. Gardner," *ibid.* p. 83.

³ L. Agassiz, "Sur quelques poissons fossiles du Brésil," Comptes Rendus, vol. xviii. (1844), pp. 1007-1015.

⁴ C. F. Hartt, 'Geology and Physical Geography of Brazil (Thayer Expedition),' 1870, chaps. xiii., xiv. *passim*.

still more recently Professor Cope¹ has described an interesting physostomous fish from an uncertain locality in South America, which is not improbably derived from the same geological formation. This appears to be the complete literature of the subject, with the exception of brief allusions to the fossils to be noted later on, and none of the accounts are accompanied by figures, if we except the single imperfect drawing given by Spix and Martius.

Though for the most part beautifully preserved, the specimens present the usual imperfections so embarrassing in palæontological research. And while some show very little traces of crushing, or are merely laterally compressed, others were subjected to considerable disturbance before the surrounding mud and sand assumed a hardened state, and several are curiously distorted. There are some in a condition that may be appropriately described as "telescoped"—the fish having been apparently subjected to pressure at right angles to its long axis; and one specimen (B.M. no. 28616) is completely folded up in a most remarkable manner.

Description.

As proved by uncrushed individuals, the body of *Rhacolepis* had a very slightly compressed form, without abdominal "keel," sometimes much elongated (as in *R. buccalis*), and sometimes relatively short (*R. latus*). The roof of the skull exhibits a corresponding flatness, and the snout is remarkably acute. The paired fins are well developed, the pelvic pair being abdominal in situation; there is a single dorsal fin in the middle of the back opposite the pelvis; the anal is small, and halfway between the pelvis and the tail; and the caudal fin is deeply forked. The scales are small or of moderate size, and the lateral line is not apparent in unabraded specimens.

Considering these various points in order, there are several features of interest in the *head* that first claim attention.

In the cranium itself, a few of the elements can be more or less distinctly recognized, but the frontals alone are sufficiently perfect and characteristic to merit special note (Plate XLVI. fig. 3). They attain the usual large dimensions and are apparently united together throughout their entire length, the anterior half of the median suture being raised into a prominent longitudinal ridge, and the bone on either side of this for some distance exhibiting a very even surface. Posteriorly, in one specimen (B. M. no. P 1957), a pair of small rectangular bones are to be observed, meeting in the middle line, and these evidently represent the parietals. There is also another prominent element in some examples—as in the original of Plate XLVII. fig. 4—which may probably be interpreted as a membrane bone above the operculum, similar to that observed in certain Characinoids.

The palatine bones are provided with teeth, as disclosed by a fracture in the skull of *R. latus* (no. P 1957); and both premaxillæ,

¹ E. D. Cope, "On two extinct forms of Physostomi of the Neotropical Region," Proc. Amer. Phil. Soc. vol. xii. (1871), p. 53.

maxillæ, and dentaries are likewise armed with a moderately powerful series. These are elongated cones, closely approximated, and varying but little in size, though those on the palatines are apparently the largest. The cleft of the mouth is slightly turned upwards, and the lower jaw scarcely projects beyond the upper; and of the two elements entering into the bony margin above, the maxillæ have much the greater extent.

But the most striking feature in the head is presented by the ring of circumorbital bones, which attain to an extraordinary size (Plate XLVI. figs. 1, 2, 5; Plate XLVII. figs. 4, 5). Two, or perhaps three, of considerable dimensions are situated behind the eye, while the largest occupies a postero-inferior position; and the anteriorly directed process of the latter, which is very narrow in *R. buccalis*, bounds the orbit below, in conjunction with the small foremost element of the ring. Posterior to this series, the long narrow preoperculum is seen; and still beyond are the other elements of the opercular fold. The operculum itself varies in form in the different species (compare Plate XLVI. figs. 1, 2; Plate XLVII. figs. 4, 5); the suboperculum is relatively large; and there is a distinct triangular interoperculum. None of these bones exhibit any definite ornament, sculpturing, or marginal denticulation, and there was no extension of the scales over any part of the cephalic region. The branchiostegal rays attached to the epihyal are about ten in number, and large and much expanded; but in front of these the ceratohyal supports an apparently equal series, which are quite of small size (Plate XLVII. fig. 1), and likewise differ in being considerably "spaced out."

The *vertebral column* is not completely shown in any specimen, and it is thus only possible to determine the number of vertebræ approximately: in *R. buccalis* there appear to be not less than 24 in the abdominal region, and perhaps as many as 20 in the caudal. The centra are well ossified, though perforated in the middle for the passage of a remnant of the notochord; and they exhibit no large lateral excavations, but are marked by delicate longitudinally extended pittings (Plate XLVI. fig. 4 a). The ribs are tolerably massive, as shown by B. M. no. 47900, and the same fossil displays a considerable number of crushed intermuscular bones. Both neural and hæmal arches in the caudal region are remarkably strong and elongate; but it is unfortunately impossible to determine with certainty the modifications for the support of the tail-fin.

In the *pectoral arch* the form of the clavicle is well shown, especially by one small fragment (no. P 1958 c). It has a gentle longitudinal curve, the concavity being anterior; and there is a comparatively broad, inwardly directed wing, in addition to the exposed part in the plane of the side of the body. The *pectoral fin* is robust (Plate XLVI. fig. 1), and the several stout rays are divided distally; but it is impossible to determine the exact number of these rays, though there cannot have been less than 18 or 20 in *R. buccalis*.

The "*pelvic*" bones are only well shown in one specimen, belonging to the small species just mentioned, and the element of the right side

is represented in Plate XLVII. fig. 3. This bone is of an elongated triangular form, the apex directed anteriorly, and the short base supporting the rays of the fin; it exhibits a little rounded process at the posterior extremity of the inner border, for articulation with its fellow of the opposite side. The *pelvic fin* is, as usual, somewhat smaller than the pectoral, though still tolerably robust; and its characters are well seen in the original of Plate XLVI. fig. 1. It is opposed to the hinder part of the dorsal, and consists entirely of soft jointed rays, to the number of about 12 in *R. buccalis*.

The *dorsal fin* is relatively short, and is supported upon a series of strong interspinous bones, of which the most anterior has the widest expansion (*R. brama*, Plate XLVI. fig. 1). In front, there are about three small spinous rays, followed by two others of larger size; but the maximum length is attained by the first succeeding soft ray, and from this there is a gradual shortening backwards. In one species, *R. latus*, the anterior soft ray is extraordinarily powerful, and divided for more than half its length by closely approximated, oblique sutures.

There is no trace of an adipose dorsal fin, notwithstanding the perfection with which some of the soft parts are preserved.

The *anal fin* is very small, and the rays in *R. buccalis* are about 10 in number; these are much divided, as shown in Plate XLVI. fig. 1.

The *caudal fin*, as already mentioned, is deeply forked, and the median rays are very short, only slightly extending beyond the much-elongated posterior termination of the body. In one specimen, indeed, probably referable to *R. buccalis* (no. P 1958 *a*), the median rays do not constitute more than a little delicate fringe, sharply marked off from the two main lobes of the fin (Plate XLVII. fig. 2), though this may quite possibly be an abnormal appearance due to the circumstances of fossilization.

The *scales* are preserved in almost every specimen, but it is only rarely that they are well displayed, owing to abrasion and fractures produced in the removal of the surrounding stony matrix. They are deeply imbricated, but it does not seem possible in any case to determine the number either of the transverse or longitudinal series; nor can anything be stated with certainty as to the variation in size in different regions. The exposed portion of each scale is beautifully ornamented with radiating ridges, which are strongest near the periphery (Plate XLVI. fig. 6); and these sometimes impart to the hinder border of dilapidated examples the appearance of being ctenoid. The superficial layer of the scales, however, is nearly always destroyed. The lateral line is only observed where the ornamented portions of the scales are broken away, and would thus not be visible in the living fish. A small "axillary appendage," of elongated form, is to be noted in one or two specimens above the pectoral fin (Plate XLVI. fig. 7). And, lastly, there is the interesting fact that the dorsal and caudal fins are covered to some extent by smaller scales than those investing the body, these being extremely thin and exhibiting no markings beyond the concentric lines of growth (B. M. no. 28616).

The eye has an ossified sclerotic capsule, and some of the soft parts of the fish are more or less indicated in nearly all the fossils. The gills are well seen when the opercular apparatus is partly removed, the lamellæ being long and slender and reaching the hinder margin of the gill-cavity. The great muscles of the side of the trunk are also fossilized; the successive myotomes, with their transverse muscular fibres, being especially distinct in one specimen in the Enniskillen Collection, which has already been referred to by Agassiz¹.

Specific Types.

In his original notice of *Rhacolepis* (misprinted "*Phacolepis*") Agassiz recognized three distinct specific types, which he very briefly defined as separated by the form of the body and the characters of the posterior elements in the circumorbital ring. These, it appears, are also readily distinguished by the shape of the operculum, and perhaps some other features; and all the examples in the British Museum may be referred to one or other of the three forms. They received the names of *R. buccalis*, *R. brama*, and *R. latus*, and figures of each are given in our Plates.

1. RHACOLEPIS BUCCALIS. (Plate XLVI. figs. 2-7; Plate XLVII. figs. 1-3.)

This is the smallest species, and comprises the fossil already mentioned as figured by Spix and Martius. It is of a very elongated shape, the greatest depth of the trunk being comprised about five and a half times in the total length. The two posterior circumorbitals are elongated and approximately of equal size, and the length of the postero-inferior plate likewise much exceeds the depth. The vertical measurement of the operculum is much greater than its antero-posterior extent, the relative proportions being about 7 : 4.

2. RHACOLEPIS BRAMA. (Plate XLVI. fig. 1; Plate XLVII. fig. 4.)

An indeterminable fragment of this species seems to have been originally noticed by Agassiz as *Amblypterus olfersii*², and the latter specific name was thus substituted for *brama* in the "Synoptical Table" in the 'Rech. Poiss. Foss.' The body is somewhat less elongate than in *R. buccalis*, the greatest depth of the fossil shown in Plate XLVI. fig. 1 being contained about four and a half times in the total length. The two posterior circumorbitals are likewise much elongated, but the lower is narrower than the upper; and the postero-inferior plate has a deep triangular form. The length and breadth of the operculum are almost equal.

3. RHACOLEPIS LATUS. (Plate XLVII. fig. 5.)

This is so called from the considerable depth of the body, as shown in the young individual figured. The two posterior circumorbitals

¹ L. Agassiz, Rech. Poiss. Foss. vol. iv. pt. i. p. 293.

² L. Agassiz, *ibid.* vol. ii. pt. i. p. 40.

are short and of equal size, and the vertical extent of the operculum is about twice its antero-posterior measure. The first soft ray of the dorsal fin is very robust and divided by numerous, closely approximated, transverse sutures.

Systematic Position.

Finally, it remains to determine the systematic position of the genus under consideration. By Agassiz¹, *Rhacolepis* was regarded as a Percoid, probably because the scales had the appearance of being ctenoid, for he had already observed the abdominal situation of the pelvic fins, which would rather point towards a relationship with other types. More recently, Dr. Günther² has quoted the genus as one of the Berycidæ; and these are the only two expressions of opinion in regard to the affinities of *Rhacolepis* that I have succeeded in discovering. A glance at the fossils now made known, however, renders it obvious that we are here concerned with a truly physostomous fish; and it is in this primitive division of the Teleostei that we must look for its nearest living representatives.

As kindly pointed out to me by Dr. Günther, some features displayed by these fossils are curiously similar to those of certain Characinoids still inhabiting the fresh waters of Brazil. The scales, for example, have an especially Characinoid aspect, and the large size of the circumorbital bones is also a prominent character of the fishes of this family. But the great number of the branchiostegal rays, the peculiarities of the tail, and the fact that these fossils are accompanied mostly by *marine* forms, are circumstances that seem to point in another direction.

The discovery of an "axillary appendage" in some of the specimens, indeed, suggests affinities with the Elopine and Chanine sections of the Clupeidæ; and it is with the first of these groups that I would venture to associate the genus. *Elops* and its allies are marine types; their bodies exhibit but little lateral compression; their posterior circumorbitals are very large; their branchiostegal rays are generally numerous; and the tail in these forms almost precisely parallels that of the ancient *Rhacolepis*. The correspondence is thus so close that there can be no doubt as to the correctness of the determination.

It is, in fact, difficult to satisfactorily distinguish the Brazilian fossil from some other Elopine genera already recognized; for, in dealing with extinct forms, the imperfection of the palæontological record often prevents any very precise comparisons. Taking first the living genera, *Megalops* may be said to differ especially in possessing a long anal fin, a distinct lateral line, and villiform teeth; while *Elops* seems to be separated by little beyond the conspicuous character of the lateral line, and the absence of small scales on the dorsal and caudal fins. Among fossil allies, *Elopopsis*³ has a more power-

¹ L. Agassiz, *Edinb. New Phil. Journ.* vol. xxx. (1841), p. 83; *Rech. Poiss. Foss.*, *Synoptical Table*, vol. i. p. xlv.

² A. Günther, 'Study of Fishes,' 1880, p. 421.

³ J. J. Heckel, 'Beitr. Kennt. foss. Fische Oesterreichs,' 1856, p. 65.

ful dentition; *Hemielopopsis*¹ seems to be distinguished, among other features, by the absence of teeth on the margin of the mouth; and *Protelops*² has relatively shorter and stouter jaws, with rounded crushing-teeth on the palatines. *Thrissopater*³ differs in having a compressed abdomen, while *Halec*⁴ and *Halecopsis*⁵ are too imperfectly known for certain reference.

Geological Age.

The foregoing conclusions become of especial interest when the geological antiquity of *Rhacolepis* is taken into consideration, for it almost certainly dates back to the Cretaceous period. As already shown by Agassiz, it is associated with other fossil fishes, *e. g.* the ganoids *Aspidorhynchus* and *Lepidotus*, and the teleostean *Cladocyclus*, the former of which are Jurassic and Cretaceous, and the latter Cretaceous, in European areas; and Gardner has recorded some remains probably of the cephalopod *Turrilites* from the same beds; so that true homotaxis (geological contemporaneity) with the Upper Cretaceous formations of the Old World appears to be well established⁶. *Rhacolepis* is thus one more of the forerunners of the Teleostei, which seem to have become developed during Jurassic times, and to have swarmed in the Chalk seas: it is one which constitutes a decided link between the old bony Ganoids and fishes of a more modern type.

EXPLANATION OF THE PLATES.

PLATE XLVI.

- Fig. 1. *Rhacolepis brama*, ♂ nat. size. [P 3986.]
 2. *Rhacolepis buccalis*, anterior portion of fish. 2 a. Transverse section of trunk. [P 3983 a.]
 3. Ditto, upper aspect of head. [P 1958.]
 4. Ditto, vertebral centra. a. Side view. b. Section. [15793, P 1962.]
 5. Ditto, posterior circumorbital bones. [P 1958 a.]
 6. Ditto, scales, twice nat. size. [15485.]
 7. Ditto, axillary appendage. [28900 b.]

¹ F. Bassani, "Descrizione dei Pesci Fossili di Lesina," Denkschr. kais. Akad. Wiss. vol. xlv. (1882), p. 215.

² G. C. Laube, "Beitr. Kennt. Fische böhm. Turon's," Denkschr. k. Akad. Wiss. vol. l. (1885), p. 286.

³ A. Günther, "Figs. & Deser. Brit. Organic Remains," Mem. Geol. Surv. dec. xiii. pl. i.

⁴ L. Agassiz, Rech. Poiss. Foss. vol. v. pt. ii. p. 123.

⁵ Undescribed specimens in British Museum.

⁶ The fossiliferous nodules also contain numerous individuals of a species of entomostracan, but this, unfortunately, does not assist in determining the precise age of the beds. It has been kindly examined by Professor Rupert Jones, F.R.S., and Mr. C. D. Sherborn, F.G.S., who regard the species as probably referable to *Cytheridea*. The former writes: "It differs from any species known to me, but in shape is near to *C. perforata*, Roemer, from the Chalk and Tertiaries."